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The breeding seasons of birds in south-western Australia

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Abstract

Data are presented on the dates when 2 703 clutches of eggs were laid by birds breeding in south-western Australia, defined as that part of Australia west of the Western Australian border and south of 26°S latitude. In all except two species, autumn breeding was rare and irregular. Over 90% of the clutches were laid between July and December inclusive. Within that overall generalisation, some more specific trends were evident.

Most species tended to lay earlier in the inland than in the south-western corner, but the trend was reversed in two species. Species taking nectar as a food source tended to breed before those taking grain. Ground insectivores bred earlier than aerial insectivores. Raptors and water birds tended to breed later than other groups.

Consideration of data for individual species showed that although each species had a characteristic breeding period, it varied regionally and from year to year in the same place. No good correlation emerged between measurement of rainfall and temperature and the onset or duration of breeding, although these factors appeared to exercise some control in some species. Rather, it seems that the timing of the birds' breeding season relates directly to the abundance of the birds' food supply and may be controlled more by the food available for parents than by potential food availability for the young.

It is pointed out that the concentration of breeding in south-western Australia into the period from July to December implies that resources are most abundant then. As a consequence, much more serious effects on the avifauna might be expected from burning in the spring than in the autumn, because it would destroy the resources which should provide food for the birds for the following twelve months.

Introduction

The time when birds breed in south-western Australia, defined as that part of the continent south of latitude 26°S and west of the Western Australian border, has attracted attention for many years. Carnaby (1946) and Serventy (1946) noted that although birds of south-western Australia normally bred in the spring, autumn nesting was observed in some years. (The terms spring and autumn refer to the seasons as understood in the Southern Hemisphere; spring is September to November, autumn is March to May). They speculated that such out of season nesting could be caused directly by out of season rainfall (with which it had been observed to correlate) or by an increase in food supply consequent upon the rainfall.

Further observations were published by Carnaby (1954), Robinson (1955) and Sedgewick (1955) which provided abundant evidence of a spring breeding period in the far south-west and occasional autumn breeding in northern areas. Following Keast and Marshall's (1954) publication of histological evidence of gonad response to rainfall in Australian arid-zone birds, Serventy and Marshall (1957) published detailed observations of two autumn breeding episodes in south-western Australia. Their data showed that the gonads of many species enlarged after cyclonic rains in March 1953 and February 1955, that the males were stimulated more than the females, that some species naturally laid eggs and reared young in the autumns following the cyclones, and that the incidence of this autumn breeding was greater in the northern parts of south-western Australia than in the more south-westerly parts. Serventy and Marshall proposed that the occurrence of spring breeding in south-western Australia during a period of increasing day length was probably coincidental. They considered that the critical stimuli to reproduction are probably environmental conditions that arise after rainfall and with the increasing temperatures that accompany the lengthening photo-period. They pointed out that low temperatures appeared to inhibit breeding and that the amount of unseasonal breeding might be related to the degree of beneficial change to the environment that followed the rain. They considered that these effects could not be observed in all birds, notably not in sea birds, and considered the possibility that the breeding response might be generated by a sudden improvement in food supply consequent upon the rain, although

they noted that the response was more rapid than they would have expected an increase in availability of food to be.

Little more was published about the breeding seasons of birds in south-western Australia for some years until Nix (1976) in an analysis of the movements and breeding of birds in Australia and New Guinea also considered the role of food supply in the control of the timing of breeding. He simulated on a computer the growth periods of plants and showed that these occurred at different times in different parts of Australia. He suggested that the factors controlling the timing of birds' breeding seasons would regulate them to coincide with the maximum food abundance. He suggested that the breeding seasons of insectivores, nectarivores, frugivores and graminivores would succeed each other just as the stages of growth of the plants succeeded each other. Taking data from Ford and Stone, (1957) who published records of breeding from Kellerberrin, he confirmed that south-western Australian species have a major breeding season in late winter and early spring which is the period most favourable for plant growth. His model showed that a smaller episode of plant growth occurred in the autumn and noted Serventy and Marshall's (1957) observations of autumn breeding.

The results of these earlier studies have demonstrated that most breeding in birds in south-western Australia occurs in the spring, but that autumn breeding does occur sometimes, associated with unseasonal autumn rain. The authors have universally accepted that an ultimate factor controlling the timing of breeding must be the birds' food supply but the early speculation that an important proximate factor timing the breeding episode was rainfall itself has gradually lost ground in favour of the speculation that the environmental effects of the rainfall may be more important. In addition, Nix (1976) has postulated a sequence of breeding that relates to the sequence of plant growth.

Three recent studies of single species are now available and show trends in individual species more clearly. Nicholls (1964, 1974) has shown that the wild individuals of the Silver Gull, *Larus novaehollandiae,* can breed successfully in both autumn and spring of the same year, and Saunders (1977) has shown the same thing for wild individuals of the Red-tailed Black Cockatoo, *Calyptorhynchus magnificus.* Davies (1977) has shown that although Zebra Finches, *Poephila guttata,* breed mainly in the spring in the northern part of south-western Australia as defined here, they do breed in the autumn if summer rains have brought up a crop of their main food, *Aristida contorta.* In spring, successful breeding correlates with high winter body weights and therefore by implication with a good food supply rather than with heavy rainfall.

Other data presented here comes from the Nest Record Scheme of the Royal Australasian Ornithologists Union and from the records of myself and my colleagues. It confirms the trends already reported and expands the numbers of species for which details can be given so that a reasonable comparison can be made between the succession of birds breeding and the sequence of plant growth, as well as allowing further interpretation of the role of rainfall and temperature in timing the breeding episodes.

Methods and material

The collection of data in the Royal Australasian Ornithologists Union Nest Record Scheme has been examined and 1 298 cards found which provide information about the dates when birds breed in south-western Australia. Cards were only accepted if they enabled the calendar month in which eggs were in the nest to be determined. If this spanned two months, the earlier was chosen. In all cases, conservative estimates of the egg-laying and incubation period were used, for these are still unknown with respect to many Australian birds. Personal records of 163 nests with eggs at Mileura, Western Australia, have been included with the RAOU nest record data.

Data on three species, the Zebra Finch, the Yellow-rumped Thornbill, *Acanthiza chrysorrhoa,* and the Black-faced Woodswallow, *Artamus cinereus,* were obtained from the original notebooks of D. L. Serventy and relate to observations made at Grass Valley, York, from 1959 to 1963, referred to in Oksche *et al.* (1963).

Observations on Black-faced Woodswallows nesting at Manmanning, on Splendid Wrens, *Malurus splendens,* nesting at Gooseberry Hill near Perth and on the Galah, *Cacatua roseicapilla,* have been contributed by Ian Rowley, and data on the nesting of White-tailed Black Cockatoos, *Calyptorhynchus baudinii,* in the Western Australian wheatbelt, have been contributed by Denis Saunders. In all cases, records have only been accepted if the calendar month in which there were eggs in the nest could be unequivocally determined.

In the analysis of these records involving comparisons amongst them, statistical methods are difficult to use, both because nest searching cannot be considered to be non-random and because the coverage of the area under consideration is not even. For example, there are abundant records from a few centres where keen ornithologists reside such as Woodanilling, Mileura, the Nullarbor Plain and Manjimup. This problem affects all studies of when birds breed, e.g. Frith and Davies (1961) and Lavery *et al.* (1968), and it is only when the raw data show overwhelming trends that reasonable certainty can be assumed. In the present study, D. L. Serventy's data from York are of great value, for the area was visited regularly each three weeks and searched systematically for nests on each visit. The trends showing up in his results should, therefore, be free from bias due to non-random searching and provide an accurate picture of the timing of breeding of these three species in the York area.

In order to analyse regional trends within south-western Australia itself, regional boundaries used by the Commonwealth Bureau of Meteorology, in their published statistics, have

been adapted and are shown in Figure 1. The Bureau of Meteorology's south-west divisions 9 and 9A correspond to the south-west division of Figure 1; its south-west divisions 8, 10 and 10A correspond to the wheatbelt division of Figure 1 and its divisions 6 (part), 7 (part), 7A, 11, 12 and 13 (part) correspond to the inland division of Figure 1. These boundaries do not correspond exactly with mean annual isohyets as shown, for example, by Nix (1976) but are quite close to the 600 mm and 350 mm isohyets, and conveniently divide the forested south-west from the cleared wheatbelt and the arid interior.

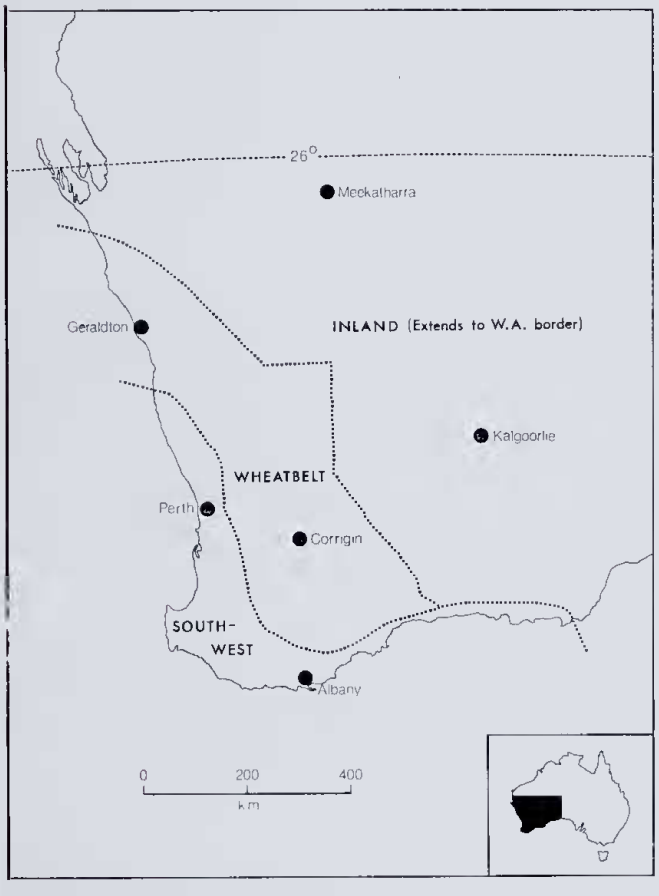

Figure 1.—Map of south-western Australia showing the three regional sub-divisions used in this paper.

Results

RAOU Nest Record Scheme and personal records from Mileura

Table 1 shows an analysis of the breeding season data available for species represented by less than 10 records. The species have been grouped by their broad ecological niche, as has become conventional in regional studies of breeding seasons (Frith and Davies 1961, Lavery *et al.* 1968). The species included under each heading are listed in Appendix I. Table 1 indicates a predominantly spring breeding season: 31% of records recorded eggs in the nest in September, 68% recorded eggs in the nest in the three spring months, and 94% recorded eggs in the nest between July and December. The sequence of nesting insectivores, nectarivores and graminivores follows that hypothesised by Nix (1976), except that aerial insectivores are considerably later than ground insectivores. Table 2 gives data for species represented by 10 to 19 records. Again there is evidence of a predominantly spring breeding season: 32% of records recorded eggs in the nest in September, 65% recorded eggs in the nest in the three spring months, and 93% of the records were of eggs in the nest between July and December. Of the individual species, those that had eggs in the nest between January and June were the aquatic Little Grebe, *Tachybaptus novaehollandiae*, and migrant Clamorous Reed Warbler, *Acrocephalus stentoreus*, both of which nested late, and a number of species in which odd individuals nested early, the White-faced Heron, *Ardea novaehollandiae* (2), Wood Duck, *Chenonetta jubata* (1), Whistling Kite, *Haliastur sphenurus* (1), Wedge-tailed Eagle, *Aquila audax* (4), Crested Pigeon, *Ocyphaps lophotes* (3), Richard's Pipit, *Anthus novaeseelandiae* (1), Black-faced Cuckoo-shrike, *Coracina novaehollandiae* (2), White-fronted Chat, *Ephthianura albifrons* (2), Australian Magpie lark, *Grallina cyanoleuca* (1), and Grey Butcherbird, *Cracticus torquatus* (1). In some cases these nests were earlier than the bulk of the population and others may best be classified as autumn nesting attempts. Tables 1 and 2 indicate a clear tendency for species of birds in south-western Australia to nest from July to December. This trend is evident even though regional differences and differences between individual years cannot be taken into account in these data.

Table 1

Breeding seasons of birds in south-western Australia (species with less than 10 records)

	J	F	M	A	M	J	J	A	S	O	N	D	Totals
Aerial Insectivores	....	....	....	....	....	....	....	1	10	4	4	3	22
Ground Insectivores....	....	....	....	1	2	1	15	28	46	29	20	4	146
Nectarivores	2	....	....	....	....	1	4	16	19	13	9	1	65
Graminivores	....	4	2	....	2	....	1	16	17	8	6	1	57
Omnivores	....	....	....	....	1	2	....	9	4	....	....	....	16
Shore and sea birds	1	....	....	....	....	....	2	4	9	4	11	4	35
Raptors	....	....	....	....	....	....	....	1	14	12	3	....	30
Water birds	3	....	....	....	....	....	....	5	5	2	10	9	34
Totals	6	4	2	1	5	4	22	80	124	72	63	22	405

Table 2

Breeding seasons of birds in south-western Australia (species with 10–19 records)

	J	F	M	A	M	J	J	A	S	O	N	D	Main data from
Little Grebe *Tachybaptus novaehollandiae*	4	2	....	....	....	....	....	....	....	3	1	4	Manjimup (8), Wooroloo (4)
White-faced Heron *Ardea novaehollandiae*	....	....	1	....	....	1	3	4	2	....	....	....	Woodanilling (5)
Mountain Duck *Tadorna tadornoides*	....	....	....	....	....	....	8	6	1	....	....	....	Woodanilling (11)
Black Duck *Anas superciliosa*	....	....	....	....	....	....	....	2	7	1	....	....	Yunderup (1), Benger (4)
Grey Teal *Anas gibberifrons*	....	....	....	....	....	....	....	2	8	2	3	....	Woodanilling (6)
Wood Duck *Chenonetta jubata*	....	....	....	....	....	....	3	2	7	1	....	1	Woodanilling (6)
Whistling Kite *Haliastur sphenurus*	....	....	....	....	....	1	....	7	....	2	....	....	Woodanilling (7)
Wedge-tailed Eagle *Aquila audax*	....	....	....	....	....	4	....	3	4	3	....	1	Mileura (9)
Brown Falcon *Falco berigora*	....	....	....	....	....	....	....	2	8	2	....	....	Nullarbor Plain (8)
Little Button-quail *Turnix velox*	....	....	....	....	....	....	....	8	2	1	1	1	Rawlinna (12)
Crested Pigeon *Ocyphaps lophotes*	....	1	2	....	....	....	....	....	5	....	3	....	Mileura (4)
Galah *Cacatua roseicapilla*	....	....	....	....	....	....	....	12	9	....	....	....	Kathleen Valley (9)
Port Lincoln Parrot *Barnardius zonarius*	....	....	....	....	....	....	....	3	5	2	....	....	Cunderdin (3), Perth (2)
Tawny Frogmouth *Podargus strigoides*	....	....	....	....	....	....	....	4	6	1	....	....	Mileura (2), Nullarbor Plain (2), Woodanilling (2)
Sacred Kingfisher *Halcyon sancta*	....	....	....	....	....	....	....	....	....	....	10	....	Katanning (3), Woodanilling (2)
Richard's Pipit *Anthus novaeseelandiae*	....	....	....	....	1	....	3	4	5	2	2	....	Woodanilling (5), Nullarbor Plain (5)
Black-faced Cuckoo-shrike *Coracina novaehollandiae*	....	....	....	1	1	....	....	3	4	5	2	1	Woodanilling (4), Nullarbor Plain (3)
Ground Cuckoo-shrike *Coracina maxima*	....	....	....	....	....	....	....	5	7	....	....	....	Nullarbor Plain (8)
White-winged Triller *Lalage sueurii*	....	....	....	....	....	....	....	....	4	4	4	1	Woodanilling (7)
Grey Shrike-thrush *Colluricincla harmonica*	....	....	....	....	....	....	1	2	6	3	....	....	Nullarbor Plain (5), Woodanilling (3)
Clamorous Reed Warbler *Acrocephalus stentoreus*	8	....	....	....	....	....	....	....	....	....	3	7	Manjimup (18)
Brown Songlark *Cinclorhampus cruralis*	....	....	....	....	....	....	9	1	....	....	....	....	Nullarbor Plain (10)
Varied Sittella *Daphoensitta chrysoptera*	....	....	....	....	....	....	....	3	2	3	2	....	Woodanilling (7)
Yellow-throated Miner *Manorina flavigula*	....	....	....	....	....	....	2	5	12	2	....	....	Woodanilling (7), Cunderdin (5)
Crimson Chat *Epthianura tricolor*	....	....	....	....	....	....	4	2	7	....	5	....	Nullarbor Plain (14)
White-fronted Chat *Epthianura albifrons*	....	....	....	1	....	1	7	2	....	....	....	....	Woodanilling (7)
Magpie Lark *Grallina cyanoleuca*	....	....	1	....	....	....	1	5	4	2	....	....	Woodanilling (5), Miling (3)
Masked Woodswallow *Artamus personatus*	....	....	....	....	....	....	....	4	2	1	10	....	Nullarbor Plain (10)
Dusky Woodswallow *Artamus cyanopterus*	....	....	....	....	....	....	....	....	....	8	9	1	Woodanilling (9), Manjimup (5)
Grey Butcherbird *Cracticus torquatus*	....	1	....	....	....	....	....	1	17	....	1	....	Coolup (10)
Totals	12	4	4	2	2	7	41	92	134	48	56	17	Grand total: 419

Table 3

(a)—Grouped breeding seasons—all birds with more than 20 records; summary by months

District	J	F	M	A	M	J	J	A	S	O	N	D	Totals
S.W.	1	....	....	....	1	7	4	25	33	38	21	11	141
Wheatbelt	....	1	....	2	10	6	18	31	32	30	14	6	150
Inland	....	2	15	12	20	14	31	87	127	19	37	....	364
Totals	1	3	15	14	31	27	53	143	192	87	72	17	655

(b)—*Breeding seasons grouped by districts; species with more than 20 cards*

Species	District	J	F	M	A	M	J	J	A	S	O	N	D	Totals
Willie Wagtail	SW	....	....	....	....	....	....	....	1	1	8	3	3	16
	Wheatbelt	....	....	....	....	....	....	....	....	5	10	2	2	19
	Inland	....	....	....	....	....	....	1	1	11	....	2	....	15
Red-capped Robin	Wheatbelt	....	....	....	....	....	....	....	5	6	5	5	....	21
	Inland	....	....	....	....	....	....	....	6	1	....	....	....	7
Black-faced Woodswallow	Wheatbelt	....	....	....	....	....	....	....	....	....	2	6	1	9
	Inland	....	....	....	....	....	....	....	....	13	2	6	....	21
Welcome Swallow	SW	....	....	....	....	....	....	....	8	13	9	6	....	36
	Inland	....	....	....	1	....	....	....	3	2	1	....	....	7
Silvereye	SW	1	....	....	....	....	....	....	....	5	3	2	2	13
	Wheatbelt	....	....	....	....	....	....	....	....	2	6	....	....	8
Magpie	SW	....	....	....	....	....	....	....	9	10	4	....	....	23
	Wheatbelt	....	....	....	....	....	....	....	9	7	3	....	....	19
Black Swan	Wheatbelt	....	....	....	....	....	....	2	3	2	....	....	....	7
	Inland	....	4	3	11	....	....	....	....	....	....	....	....	18
Banded Plover	Wheatbelt	....	....	....	1	4	....	6	2	2	1	....	....	16
	Inland	....	....	....	....	1	1	6	8	....	....	....	....	16
Australian Dotterel	Wheatbelt	....	1	....	1	6	2	1	1	....	....	....	....	12
	Inland	....	1	....	....	2	4	8	2	....	....	1	....	18
Coot	SW	5	....	....	....	....	....	....	....	1	4	9	9	28
Red Wattlebird	SW	....	....	....	....	1	1	1	2	6	3	....	....	14
Raven	Wheatbelt	....	....	....	....	....	4	6	6	3	....	....	....	19*
Kestrel	Inland	....	....	....	....	....	....	....	5	50	4	3	....	62
White-browed Babbler	Inland	....	....	1	3	2	1	3	3	7	....	3	....	23
Zebra Finch	Inland	....	1	10	5	2	6	7	16	13	12	22	....	94
Little Crow	Inland	....	....	....	....	....	3	6	41	26	....	....	....	76
Totals		3	15	14	29	22	47	131	186	77	70	17	6	617

*One card from the SW.

For those species represented in the records by 20 or more cards, regional differences can be examined. The data are presented in Table 3. Table 3(a) presents the grouped results: 29% recorded eggs in the nest in September, 64% recorded eggs in the nest in the three spring months, and 86% recorded eggs in the nest between July and December. Looking at regional differences, the percentage of records of eggs in the nest in September was 23, 21 and 35 for the south-west, wheatbelt and inland respectively. This was the highest percentage of any month for the inland but in the wheatbelt and south-west, the spread was more even over August, September and October and in the south-west a slightly higher percentage occurred in October (27%) although the difference is small.

The data for individual species with sufficient records for at least one region to be considered separately are shown in Table 3(b), and the trends are easier to see. The Willie Wagtail, *Rhipidura leucophyrs*, Red-capped Robin, *Petroica goodenovii*, and Black-faced Woodswallow tend to nest earlier in the inland than in either the wheatbelt or the south-west. The Australian Magpie, *Gymnorhina tibicen* and Silvereye, *Zosterops lateralis*, do not show differences between wheatbelt and south-west although the Silvereye appears to have a more extended breeding season in the south-west than the wheatbelt. On the other hand, both the Banded Plover, *Vanellus tricolor* and the Australian Dotterel, *Peltohyas australis*, tend to nest a little earlier in the wheatbelt than the inland. There are insufficient data from the other species to compare regions.

A second important phenomenon begins to emerge in Table 3. Some species characteristically breed both between January and June and between July and December whilst others breed only between July and December. Thus all the nests of the Willie Wagtail, Red-capped Robin, Black-faced Woodswallow, Australian Magpie and Nankeen Kestrel, *Falco cenchroides*, occur between July and December. A few Australian Ravens, *Corvus coronoides*, and Little Crows, *Corvus bennetti*, nested in June and one Silvereye and a few Coots, *Fulica atra*, were recorded with eggs in the nest in January, but otherwise these four species only nested between July and December. In other species some nests were recorded between January and June but in these cases there were fewer nests between January and June than between July and December. These species were (figures in parentheses compare nests in first and second half of the year): Banded Plover (7:25), Welcome Swallow, *Hirundo neoxena* (1:42), Red Wattlebird, *Anthochaera*

Table 4

Breeding seasons (number of nests with eggs) of three passerines at York over five seasons (data from D. L. Serventy)

Species/Year	No. of Visits	M	J	J	A	S	O	N	D	J	F	M	A	M	Totals	Autumn nests
Zebra Finch *Poephila guttata*—																
1959–60	14	....	....	....	....	1	11	4	....	....	1	1	4	1	23	7
1960–61	17	....	....	....	....	1	3	2	2	7	3	1	4	....	23	15
1961–62	17	....	....	....	....	....	1	6	5	2	1	..	....	....	15	3
1962–63	17	....	....	....	1	....	....	3	2	1	1	4	3	....	15	9
1963–64	18	....	....	....	....	1	2	3	....	....	3	0	1	2	12	6
Totals	....	....	....	....	1	3	17	18	9	10	9	6	12	3	88	40
Yellow-rumped Thornbill *Acanthiza chrysorrhoa*—																
1959–60	14	....	....	....	....	2	4	1	....	....	....	....	....	....	7	....
1960–61	17	....	1	4	3	1	2	4	....	....	....	....	....	....	15	....
1961–62	17	....	....	....	2	4	3	3	....	....	....	....	....	....	12	....
1962–63	17	....	....	....	5	1	3	....	....	....	....	....	....	....	9	....
1963–64	18	1	....	1	....	....	....	....	....	....	....	....	....	....	2	....
Total	....	1	1	5	10	8	12	8	....	....	....	....	....	....	45	....
Black-faced Woodswallow *Artamus cinereus*—																
1959–60	14	....	....	....	....	....	1	1	1	1	....	....	....	....	4	1
1960–61	17	....	....	....	....	....	....	3	1	....	....	....	....	....	4	....
1961–62	17	....	....	....	....	....	1	4	4	....	....	....	....	....	9	....
1962–63	17	....	....	....	....	....	....	....	1	....	....	....	....	....	1	....
1963–64	18	....	....	....	....	....	....	....	...	....	....	....	....	....	0	....
Totals	....	....	....	....	....	....	2	8	7	1	....	....	....	....	18	1

carunculata (2:12), White-browed Babbler, *Pomatostomus superciliosus* (7:16) and Zebra Finch (24:70). Two species stand apart. The Australian Dotterel appears to be predominantly an autumn and winter nesting species, both in the wheatbelt and the inland and the Black Swan, *Cygnus atratus*, has been recorded nesting in the autumn in the inland and the late winter, early spring in the wheatbelt. Further data collected by Tingay *et al.* (1977) indicate that it nests in the late winter in the south-west.

Other data

Grass Valley, York.—D. L. Serventy's data are presented in Table 4 and show that each species has a characteristic breeding pattern. The Zebra Finch shows a large peak of nests with eggs in October and November, and a smaller peak in April. This resembles the data for that species shown in Table 3, but the start of intense spring nesting is earlier in the inland than in the wheatbelt at York. On the other hand, summer nests occur in the wheatbelt whereas they are rare in the inland. Most nests of the Yellow-rumped Thornbill were recorded in August, September and October and most of the Black-faced Woodswallow nests were in November and December, in agreement with the trend shown in Table 3(b) for this species to nest later in the wheatbelt than at inland sites.

Differences between years are evident. In 1959-60 and 1963-64, the Zebra Finch had well separated spring and autumn breeding seasons. In 1961-62 breeding was over in February, and the species effectively bred only in the spring. On the other hand, in 1962-63, most of the breeding was in the summer and autumn, and in 1960-61 breeding was continual from September to April.

The total monthly rainfall at York is shown in Figure 2. It is not easy to find direct correlations between rainfall and the breeding of Zebra Finches. The total nests found in the study area each season correlates positively (Spearman's $r = +0.95$; $P < 0.05$) with the total rainfall in January of the year in question, but it is not easy to accept this as a valid correlation, for in some years, e.g. 1961-62, the bulk of the nesting is over by January. There seems to be no clear association between the start or end of the winter rain period and the start of the breeding season, nor between summer rainfall and the presence of summer breeding. In Figure 2, the mean monthly temperatures recorded at Perth are shown. Although this locality is 100 km west of York, the trend shown in a comparison across years would be similar in the two sites. There is no clear correlation between temperature and the pattern of breeding shown by the Zebra Finches. It is likely, therefore, that the birds are not responding directly to these environmental factors, although the timing of breeding may be controlled by the indirect effects of environmental changes.

The same statement may be made about the breeding of the Yellow-rumped Thornbill and the Black-faced Woodswallow. In both there are differences between years but in neither do these differences relate directly to differences between rainfall and temperature patterns in the corresponding years. Yellow-rumped Thornbills bred early in 1960-61 and 1963-64 and in 1963-64 failed to breed at all in their normal spring period. In comparison with Ford's data from Bibra Lake, Perth (Ford, 1963) for some of the same years (1959 and 1961) this species bred one to two months earlier at York than on the coast. The Black-faced Woodswallows bred consistently

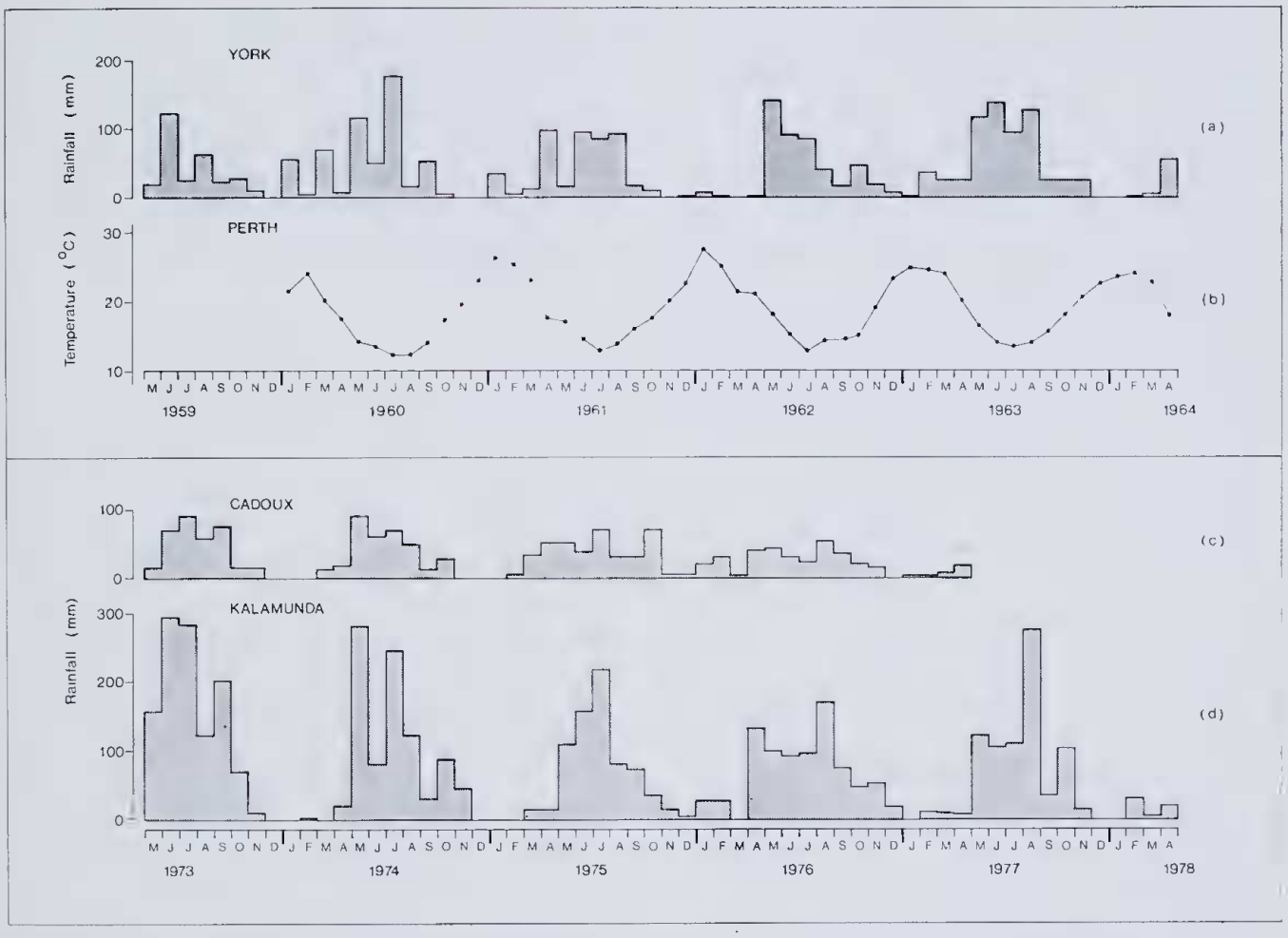

Figure 2.—Environmental data for three sites at which breeding data were collected. (a) Monthly rainfall totals for York. (b) Mean monthly temperatures for Perth. (c) Monthly rainfall totals for Cadoux. (d) Monthly rainfall totals for Kalamunda.

in late spring, early summer, but in 1962-63 and in 1963-64 only one nest was found in the study area, and breeding did not seem to have taken place.

Serventy's data, therefore, indicate that in one place, each species has a characteristic breeding time, but that the precise timing varies from year to year. Further, the changes in timing with different years do not correlate between species. Thus the Zebra Finch bred early in 1959-60 but late in 1960-61, whereas the reverse was true for the Yellow-rumped Thornbill.

Manmanning.—Rowley's data for the Black-faced Woodswallow are presented in Table 5 and show that breeding is a month earlier than for the same species at York. Again there are differences between individual years both in timing and extent of the breeding period. The mean monthly rainfall at Cadoux, 8 km north of Manmanning is shown in Figure 2. There is no clear correlation between differences in the timing and extent of the breeding season in individual years and differences in the pattern of precipitation in corresponding years.

Table 5

Breeding data from Rowley for two species of birds in south-western Australia. (Number of nests with eggs.)

Years	Month					Total
	S	O	N	D	J	
(a) Black-faced Woodswallow, Manmanning.						
1973–74	....	3	7	3	2	15
1974–75	....	8	14	3	....	25
1975–76	....	3	12	....	....	15
1976–77	....	8	4	....	....	12
Totals	....	22	37	6	2	67
(b) Splendid Wren, Gooseberry Hill, Kalamunda.						
1973–74	....	2	3	2	....	....	7
1974–75	....	1	8	3	3	1	16
1975–76	....	.	5	5	2	....	12
1976–77	....	7	3	1	....	....	11
1977–78	....	1	3	3	1	1	9
Totals	....	11	22	14	6	2	55

Gooseberry Hill.—Rowley's data for the Splendid Wren show large differences between years in both the timing and extent of breeding. Rainfall figures for nearby Kalamunda are presented in Figure 2 and again no correlation is evident. There is a general trend for the species to nest at the end of the wet winter, but detailed correlations do not occur.

Galah.—Rowley's data for the Galah are presented in Table 6. The data were collected at three sites, Manmanning and Coomalloo in the south-west division and Mileura in the inland division. Galahs show considerable constancy in the timing of the nesting season from year to year and region to region. Where differences between years occur, Manmanning and Coomalloo differ in the same direction. At both sites the month in which most nests were started was August in 1971 and 1974 and September in 1972 and 1973. The data from Mileura are not extensive but do indicate a concentration of nesting in the August-September period. Overall 90% of the 581 Galah nests were started in August or September.

Table 6

Breeding data from Rowley for the Galah from three sites in south-western Australia. The figures indicate the number of nests started each month

	Year	J	F	M	A	M	J	J	A	S	O	N	D	Total
Coomalloo Creek	1971	....	....	....	....	....	....	....	23	4	5	....	....	32
	1972	....	....	....	....	....	....	....	7	15	4	....	....	26
	1973	....	....	....	....	....	....	....	4	12	2	....	....	18
	1974	....	....	....	....	....	....	2	23	4	1	....	....	30
Manmanning	1971	....	....	....	....	....	....	1	68	26	8	....	....	103
	1972	....	....	....	....	....	....	....	16	67	11	....	....	94
	1973	....	....	....	....	....	....	....	43	53	14	....	....	110
	1974	....	....	....	....	....	....	....	88	28	6	....	....	122
Mileura	1971	....	....	....	....	....	....	1	14	6	2	....	....	23
	1972	....	....	....	....	....	....	....	14	2	....	....	....	16
	1974	....	....	....	....	....	....	....	5	2	....	....	....	7
Totals		....	....	....	....	....	....	4	305	219	53	....	....	581

White-tailed Black Cockatoo.—Table 7 presents Saunders data for the breeding seasons of this species at four different localities in south-western Australia. All, except Coomalloo Creek (south-west) are in the wheatbelt division of the State. Overall differences are apparent in the timing of breeding. The most northerly locality, Coomalloo Creek, is earliest even though it is in the south-west division, and the most southern locality, Moornaming, is latest, with Manmanning and Tarwonga in an intermediate position. There are differences too between individual years at each locality. Saunders (1979) discusses these differences and can find no clear correlation between environmental variables and the timing of breeding in this species.

Table 7

Breeding data from Saunders (number of nests with eggs) of the White-tailed Cockatoo in four localities in south-western Australia

	Year	M	J	J	A	S	O	N	D	J	F	M	A	Total
Coomalloo Creek	1969	....	....	3	5	1	....	....	....	....	....	....	....	9
	1970	....	....	....	10	13	5	....	....	....	....	....	....	28
	1971	....	....	15	30	9	1	....	....	....	....	....	....	55
	1972	....	....	....	25	37	3	....	....	....	....	....	....	65
	1973	....	....	4	43	19	8	....	....	....	....	....	....	74
	1974	....	....	13	37	13	11	1	....	....	....	....	....	75
	1975	....	....	10	39	23	9	1	....	....	....	....	....	82
	1976	....	....	2	27	28	7	....	....	....	....	....	....	64
	1977	....	....	....	8	31	2	....	....	....	....	....	....	41
Manmanning	1969	....	....	1	2	2	1	....	....	....	....	....	....	6
	1970	....	....	....	3	12	3	....	....	....	....	....	....	18
	1971	....	....	....	12	8	2	....	....	....	....	....	....	22
	1972	....	....	....	....	11	2	....	....	....	....	....	....	13
	1973	....	....	....	3	5	6	....	....	....	....	....	....	14
	1974	....	....	....	7	6	....	....	....	....	....	....	....	13
	1975	....	....	....	4	6	....	....	....	....	....	....	....	10
	1976	....	....	....	3	3	....	....	....	....	....	....	....	6
	1977	....	....	....	....	....	....	....	....	....	....	....	....	0
Tarwonga	1969	....	....	1	4	1	3	....	....	....	....	....	....	9
	1970	....	....	....	1	5	7	....	....	....	....	....	....	13
Moornaming	1969	....	....	....	2	4	....	....	....	....	....	....	....	6
	1970	....	....	....	....	13	2	1	....	....	....	....	....	16
Totals		....	....	49	265	250	72	3	....	....	....	....	....	639

Mileura.—Davies (1977) has presented breeding data for the Zebra Finch at this inland site which may be compared with Serventy's data from York, a wheatbelt site. The pattern of breeding exhibited by the species is similar, with breeding taking place in the spring and to a lesser extent throughout summer and autumn, but varying in its precise timing from year to year. There was some evidence that chicks raised from autumn nestings survived less well than those raised during spring nestings.

Discussion

The results presented above show that the birds of south-western Australia tend to breed between July and December, predominantly in the spring months. Within that overall generalisation, some specific trends are evident. Although many species breed only in the spring, some also exhibit autumn breeding activities, as discussed at length by Serventy and Marshall (1957). In most cases these autumn breeding episodes are quantitatively smaller than the equivalent spring ones, but for the Australian Dotterel throughout the region, and the Black Swan in the inland, autumn breeding appears to be the dominant pattern. Regional trends also appear. In general, species breed earlier inland than in the wheatbelt or south-west. The two plovers are interesting, however, in that both breed earlier in the wheatbelt than the inland and the northern populations of White-tailed Black Cockatoos breed earlier than the southern ones.

Clear variations in the timing of breeding for individual species from year to year, suggest that photoperiod itself is not always a major determinant. Serventy and Marshall (1957) have already stressed this point. They consider that the critical stimuli to reproduction are probably environmental conditions that arise after rainfall and with relatively high temperatures that accompany the lengthening photoperiod. They also considered low temperatures to be important as a breeding inhibitor.

South-western Australia experiences a winter rainfall climate in which heavy rain is rare between November and March. The trend of south-western species to breed between July and December is, therefore, consistent with Serventy and Marshall's hypothesis, for in most years the spring is the only period following heavy rain that is also warm. Such a general hypothesis cannot be expected to apply to all species and the White-browed Babbler, Banded Plover and Australian Dotterel all nest in the winter, a cold wet period. Probably these ground-feeding insectivorous birds find food with difficulty in dry weather, but with much greater ease as the insects become active after rain. They may, therefore, be responding either to the rain, or the environmental effects of it or simply to the increased food supply.

The year to year variation in the detailed data given for the Zebra Finch, Yellow-rumped Thornbill, Black-faced Woodswallow, Splendid Wren, Galah and White-tailed Black Cockatoo show that each species must be considered separately in relation to environmental factors and that no simple relationships are evident between rainfall and breeding response.

Marshall (1961) reviews work that suggests that the timing of breeding episodes is correlated with ensuring a good food supply for the young. Much of the work up to that time sought to establish correlations between the onset of breeding and environmental variables that might precede such abundant food supplies for the young, although they may not themselves be causally related to increasing this food supply. More recently, Perrins (1970) discussed the role of food in the timing of breeding and concluded that the evidence, although not yet overwhelming, was tending to implicate the food supply of adults, particularly of the females, as an important proximate factor controlling the onset of birds' breeding. Recent work by Jones and Ward (1976) on the Red-billed Quelea, *Quelea quelea*, suggests that its breeding episodes may be timed more precisely by direct relationships between the present food supply for potential parents rather than the future food supply for young.

Some of the detailed studies of breeding in south-western Australian birds that have been published, show correlations between good supplies of food for the parents and breeding episodes. Nicholls' (1964, 1974) studies of the timing of breeding of the Silver Gull showed that there are eggs continuously on Carnac Island, off Perth, throughout the autumn, winter and spring, with little egg-laying in the winter. Very little laying occurs in summer. The food supplies of Silver Gulls in metropolitan Perth come largely from the suburban rubbish tips and offal sites adjacent to slaughter yards. These are available throughout the year. Studies by Nicholls of captive gulls showed that young chicks hatched in the summer died of heat, and if this effect operated in the wild, as it almost certainly does, there would be strong selection against gulls breeding in the summer, because energy would be wasted in a regularly unsuccessful breeding attempt. Silver Gulls, therefore, breed throughout that part of the year when chicks will survive. They have a nearly constant, plentiful food supply and the lack of winter egg-laying is probably a consequence of the nearly simultaneous start of breeding by gulls in April-May, that involves them in parental duties for the next three months. The only winter eggs would come from second breeding attempts by failed breeders.

Saunders (1977) studying the Red-tailed Black Cockatoo, showed that it bred in both spring and autumn. This species has taken to eating the fruits of an introduced weed, *Emex australis*, almost exclusively and the double breeding season may also reflect an abundant and constant food supply.

At Mileura, Davies (1977) was able to show that Zebra Finches bred in warm periods, especially the spring, in years of effective summer rainfall when the birds' food supply of grass had germinated, established and seeded well. In three years studied there was little successful breeding in one year and much successful breeding in two.

In the year of little breeding the birds' winter weights were lower than in the other two years, suggesting that the condition of the parents may be a factor determining whether or not breeding occurs. The Zebra Finch definitely did not respond by breeding after any rainy episode. The young hatched in the autumn appeared not to survive as well as those hatched in the spring, and from an evolutionary point of view may seem unimportant. On the other hand, Zebra Finch populations sustain great fluctuations, and potentially have a very high rate of increase, so that the survival of even a few birds might, in certain years, make the difference between the survival and recovery of the local population, or its total extinction. In such circumstances even a small autumn breeding episode could be important in giving a depleted population additional recruits for a spring-breeding period.

The Willie Wagtail (Table 3(b)) and Black-faced Woodswallow (Tables 3(b) and 4) are both aerial insectivores and tend to breed later than the ground insectivores, the Yellow-rumped Thornbill (Table 4) and the Red-capped Robin (Table 3(b)). This appears to correlate well with the activity of their prey, for whereas ground-dwelling insects become active as the soil wets with the first rains, the flying insects are not abundant until the weather warms up and the growth and resting stages metamorphose and begin flying. The aerial insectivores are correspondingly later in breeding than the ground insectivores. Detailed studies of individual species are needed to resolve this issue.

An interesting case is the White-tailed Black Cockatoo (Table 5) which lays early in the spring. It feeds on the fruits of Proteaceae which are available at that time. However, a second factor probably operates here, for the bird has a very long incubation and nestling period (Saunders pers. comm. 1978). Young are sometimes desiccated by the heat of summer if they have not left the nest by the end of November, and there would be in these cockatoos, as in the seagulls, strong selective pressures against starting nesting attempts late in the year. It is important to view this restraint in perspective for the distribution of these cockatoos is probably limited to areas where there is sufficient food available early in the year for them to start nesting in time to get the young out of the nest before the hot weather begins.

A clear assessment of the importance of the role of parental food supply as opposed to environmental variables in timing the initiation of breeding episodes of south-western Australian birds must await more data and preferably experimental work for which there is now ample field information to ensure unequivocal experimental design. Nonetheless one important conclusion can be drawn from this survey. The breeding seasons of south-western Australian birds are concentrated between July and December and occur particularly in the spring. Because there seems to be a clear correlation between the time birds breed and an abundant food supply, either for parents or young, it follows that the food resources on which these birds depend are particularly abundant then, and this abundance also provides a store on which they will draw for the rest of the year. If this store is destroyed, as it would be by burning off in the spring, not only will their breeding effort be jeopardised, but their store of future food will also be damaged. Although Christensen and Kimber (1975) have found that bird populations are not greatly disturbed by burning, it is clear from the present review that spring burning must be much more damaging than autumn burning. Further, as many birds feed on invertebrates, at least part of this food store must represent a peak of abundance of invertebate life, so that burning in the spring would damage the productivity and perhaps the variety of the invertebrate fauna even more severely than it would bird populations.

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Appendix I

Raptors

Osprey	*Pandion haliaetus*
Black-shouldered Kite	*Elanus notatus*
Brown Goshawk	*Accipiter fasciatus*
Coliared Sparrowhawk	*Accipiter cirrhocephalus*
Wedge-tailed Eagle	*Aquila audax*
Little Eagle	*Hieraaetus morphnoides*
Spotted Harrier	*Circus assimilis*
Swamp Harrier	*Circus aeruginosus*
Peregrine Falcon	*Falco peregrinus*
Spotted Owl	*Ninox novaeseelandiae*
Barn Owl	*Tyto alba*
Kookaburra	*Dacelo novaeguineae*

Aerial insectivores

Tawny Frogmouth	*Podargus strigoides*
Owlet-nightjar	*Aegotheles cristatus*
Spotted Nightjar	*Caprimulgus guttatus*
Rainbow Bee-eater	*Merops ornatus*
White-backed Swallow	*Cheramoeca leucosternum*
Tree Martin	*Cecropis nigricans*
Fairy Martin	*Cecropis ariel*
Little Woodswallow	*Artamus minor*

Ground insectivores

Bush Stone-curiew	*Burhinus magnirostris*
Pallid Cuckoo	*Cuculus pallidus*
Black-eared Cuckoo	*Chrysococcyx osculans*
Rufous-tailed Bronze-cuckoo	*Chrysococcyx basalis*
Shining Bronze-cuckoo	*Chrysococcyx lucidus*
Southern Scrub-robin	*Drymodes brunneopygia*
Scarlet Robin	*Petroica multicolor*
Hooded Robin	*Melanodryas cucullata*
White-breasted Robin	*Eopsaltria georgiana*
Western Yellow Robin	*Eopsaltria griseogularis*
Jacky Winter	*Microeca leucophaea*
Crested Shrike-tit	*Falcunculus frontatus*
Gilbert Whistler	*Pachycephala inornata*
Golden Whistler	*Pachycephala pectoralis*
Rufous Whistler	*Pachycephala rufiventris*
Crested Bellbird	*Oreoica gutturalis*
Restless Flycatcher	*Myiagra inquieta*
Cinnamon Quail-thrush	*Cinclosoma cinnamomeum*
Nullarbor Quail-thrush	*Cinclosoma alisteri*
Grey-crowned Babbler	*Pomatostomus temporalis*
Little Grassbird	*Megalurus gramineus*
Splendid Wren	*Malurus splendens*
Red-winged Wren	*Malurus elegans*
White-winged Wren	*Malurus leucopterus*
Rufous-crowned Emu-wren	*Stipiturus ruficeps*
White-browed Scrubwren	*Sericornis frontalis*
Redthroat	*Sericornis brunneus*
Weebill	*Smicrornis brevirostris*
Western Warbler	*Gerygone fusca*
Broad-tailed Thornbill	*Acanthiza apicalis*
Chestnut-rumped Thornbill	*Acanthiza uropygialis*
Samphire Thornbill	*Acanthiza iredalei*
Southern Whiteface	*Aphelocephala leucopsis*
White-browed Treecreeper	*Climacteris affinis*
Rufous Treecreeper	*Climacteris rufa*
Striated Pardalote	*Pardalotus striatus*

Omnivores

Emu	*Dromaius novaehollandiae*
Spotted Bowerbird	*Chlamydera maculata*
Pied Butcherbird	*Cracticus nigrogularis*
Grey Currawong	*Strepera versicolor*
Torresian Crow	*Corvus orru*

Graminivores

Stubble Quail	*Coturnix pectoralis*
Painted Button-quail	*Turnix varia*
Laughing Dove	*Streptopelia senegalensis*
Diamond Dove	*Geopelia cuneata*
Common Bronzewing	*Phaps chalcoptera*
Crested Pigeon	*Ocyphaps lophotes*
White-tailed Black Cockatoo	*Calyptorhynchus baudinii*
Regent Parrot	*Polytelis anthopeplus*
Budgerygah	*Melopsittacus undulatus*
Red-capped Parrot	*Purpureicephalus spurius*
Western Rosella	*Platycercus icterotis*
Many-coloured Parrot	*Psephotus varius*
Blue Bonnet	*Northiella haematogaster*
Bourke's Parrot	*Neophema bourkii*
Elegant Parrot	*Neophema elegans*
Painted Firetail	*Emblema picta*

Nectarivores

Purple-crowned Lorikeet	*Glossopsitta porphyrocephala*
Little Wattlebird	*Anthochaera chrysoptera*
Spiny-cheeked Honeyeater	*Acanthagenys rufogularis*
Singing Honeyeater	*Lichenostomus virescens*
Purple-gaped Honeyeater	*Lichenostomus cratitius*
Yellow-plumed Honeyeater	*Lichenostomus ornatus*
Grey-fronted Honeyeater	*Lichenostomus plumulus*
White-plumed Honeyeater	*Lichenostomus penicillatus*
Brown-headed Honeyeater	*Melithreptus brevirostris*
White-naped Honeyeater	*Melithreptus lunatus*
Brown Honeyeater	*Lichmera indistincta*
New Holland Honeyeater	*Phylidonyris novaehollandiae*
White-cheeked Honeyeater	*Phylidonyris nigra*
White-fronted Honeyeater	*Phylidonyris albifrons*
Tawny-crowned Honeyeater	*Phylidonyris melanops*
Western Spinebill	*Acanthorhynchus superciliosus*
Pied Honeyeater	*Certhionyx variegatus*

Waterbirds

Great Crested Grebe	*Podiceps cristatus*
Hoary-headed Grebe	*Poliocephalus poliocephalus*
Darter	*Anhinga melanogaster*
Little Pied Cormorant	*Phalacrocorax melanoleucos*
Black Cormorant	*Phalacrocorax carbo*
Little Black Cormorant	*Phalacrocorax sulcirostris*
White-necked Heron	*Ardea pacifica*
Large Egret	*Egretta alba*
Nankeen Night-heron	*Nycticorax caledonicus*
Freckled Duck	*Stictonetta naevosa*
White-eyed Duck	*Aythya australis*
Musk Duck	*Biziura lobata*
Black-tailed Native-hen	*Gallinula ventralis*
Dusky Moorhen	*Gallinula tenebrosa*
Swamphen	*Porphyrio porphyrio*

Shore and sea birds

Little Penguin	*Eudyptula minor*
Australian Pelican	*Pelecanus conspicillatus*
Black-faced Cormorant	*Phalacrocorax fuscescens*
Pied Oystercatcher	*Haematopus ostralegus*
Hooded Dotterel	*Charadrius rubricollis*
Black-fronted Dotterel	*Charadrius melanops*
Silver Gull	*Larus novaehollandiae*
Caspian Tern	*Hydroprogne caspia*
Roseate Tern	*Sterna dougalii*
Bridled Tern	*Sterna anaethetus*
Crested Tern	*Sterna bergii*